Zoosyst. Evol. 101 (3) 2025, 1187–1195 | DOI 10.3897/zse.101.148504

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Integrative taxonomy reveals two new species of *Ligidium* (Crustacea, Isopoda, Oniscidea) from China

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https://zoobank.org/F5710833-8C0D-4E5B-93D0-ECB117404C0C

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Academic editor: Luiz F. Andrade ♦ **Received** 2 February 2025 ♦ **Accepted** 22 May 2025 ♦ **Published** 10 July 2025

Abstract

Ligidium is the most species-rich genus within the family Ligiidae. In morphological taxonomy, some species are often difficult to identify due to their high morphological similarity. This study evaluates the taxonomic status of nine similar *Ligidium* species by combining morphological examination with molecular phylogenetic analyses based on two mitochondrial genes (*COI*, *12S rRNA*). Two new species – *Ligidium alpinum* Li & Jiang, **sp. nov.** and *L. cuspidatum* Li & Jiang, **sp. nov.** – are described from China. Morphological photographs of the new species and three maps showing the geographic distribution patterns of *Ligidium* species are provided.

Key Words

Ligiidae, mitochondrial DNA, morphology, phylogenetic analyses, taxonomy

Introduction

Ligidium Brandt, 1833, was established by Brandt (1833), with *L. persoonii* Brandt, 1833 (a junior synonym of *Oniscus hypnorum* Cuvier, 1792) as the type species. It is the most species-rich genus within the family Ligiidae Leach, 1814. To date, a total of 65 *Ligidium* species have been recorded worldwide (Schmalfuss 2003; WoRMS 2024; Recuero and Caterino 2025). Before this study, seventeen species had been reported from China (Kwon and Taiti 1993; Wang and Kwon 1993; Nunomura and Xie 2000; Li 2015, 2017; Wang et al. 2022).

In morphological taxonomy, the male pleopod 2 endopod has been confirmed as the most important character for distinguishing species of *Ligidium* (Sfenthourakis 1993; Klossa-Kilia et al. 2006; Li 2017; Yoshino and Kubota 2022). However, the same species at different ages or localities often exhibit subtle differences in the morphology of the male pleopod 2 endopod (Strouhal 1971; Yoshino and Kubota 2018). As new *Ligidium* species continue to be discovered, morphological similarities have become increasingly pronounced (Yoshino and Kubota 2022). Thus, distinguishing similar species based on morphological traits alone is becoming increasingly challenging.

In recent years, the integration of morphological and molecular data has significantly contributed to the discovery of new woodlouse species (Gongalsky et al. 2021; Raupach et al. 2022; Jiang et al. 2024). Mitochondrial markers, particularly *COI* and *12S rRNA*, have proven effective for species delimitation within *Ligidium* (Li 2017; Wang et al. 2022; Recuero and Caterino 2025). In this work, we identify *Ligidium* specimens exhibiting minor differences in the male pleopod 2 endopod and aim to

evaluate whether these differences represent interspecific divergence or intraspecific variation. We describe new *Ligidium* species based on morphological evidence, supported by molecular phylogenetic analyses.

Materials and methods

Sampling collection, morphologic preparation, and identification

Specimens for this study were collected using tweezers, fixed in 100% ethanol, and stored in the Insect Museum, Jiangxi Agricultural University, Nanchang, China (JXAUM).

Appendage dissection and mounting followed the methods described in Wang et al. (2024). Line drawings were prepared using the GNU Image Manipulation Program (Montesanto 2015). Morphological terminology follows Wang et al. (2022).

PCR amplification and sequencing

DNA extraction, amplification, and sequencing followed Wang et al. (2022). All sequences were deposited in the International Nucleotide Sequence Database Collaboration (INSDC) via the DNA Data Bank of Japan (DDBJ), and the accession numbers are listed in Suppl. material 1.

Phylogenetic analyses

MAFFT v7.313 (Katoh and Standley 2013) was used to align the concatenated sequences (including outgroups). Bayesian inference (BI) and maximum likelihood (ML) analyses were conducted using MrBayes v3.2.6 (Ronquist et al. 2012) and IQ-TREE v2 (Minh et al. 2020), respectively, on the PhyloSuite platform (Zhang et al. 2020). For BI analyses, four Markov chain Monte Carlo (MCMC) chains were run simultaneously for 10 million generations. The sampling frequency was set to 1000, with a burn-in fraction of 0.25. Posterior probabilities (PP) are indicated on the consensus tree. Convergence was confirmed by an average standard deviation of split frequencies below 0.01 and a potential scale reduction factor close to 1.0. In ML analyses, 1000 bootstrap replicates were conducted. ModelFinder was used to determine the best-fit substitution models for each gene partition under the Bayesian information criterion (Kalyaanamoorthy et al. 2017). The HKY+F+I+G4 and TPM2u+F+I+G4 models were selected for BI and ML analyses of the concatenated genes, respectively. The following species were used as outgroups for phylogenetic reconstruction: *Armadillidium vulgare* Latreille, 1804; *Tylos ponticus* Holmes & Gay, 1909; *Procellio scaber* Latreille, 1804; *Spherillo dorsalis* Iwamoto, 1943; and *Cubaris murina* Brandt, 1833. Accession numbers are provided in Suppl. material 1. Outgroup sequences were sourced from Hurtado et al. (2014) and Raupach et al. (2022). The resulting gene phylogenies were visualized using iTOL v5 (Letunic and Bork 2021).

Results

Morphological analysis

Nine *Ligidium* members were identified based on external traits and the structures of dissected appendages. Among them, we recognized two putative new species from Jiangxi Province and Sichuan Province, China. The species from Jiangxi is similar to *L. hypnorum*, *L. acuminatum*, and *L. tridentatum* in having a straight distal part in the male pleopod 2 endopod. It can be distinguished by the presence of four spines at the distal apex of the male pleopod 2 endopod. In *L. hypnorum* and *L. acuminatum*, the male pleopod 2 endopod lacks spines, while *L. tridentatum* has three spines at the subapical apex of the male pleopod 2 endopod (Jackson 1923; Wang et al. 2022). The species from Sichuan is similar to *L. denticulatum*, *L. deltodontum*, *L. gracilentum*, and *L. sichuanense* in possessing a tooth at the distal part of the male pleopod 2 endopod. It can be distinguished by the presence of two small spines on the inner margin of the distal part of the male pleopod 2 endopod. In the latter four species, the distal part of the male pleopod 2 endopod lacks spines on the inner margin (Shen 1949; Nunomura 2002). Although these two species can be distinguished from their congeners by the refined structures of the male pleopod 2 endopod, it remains uncertain whether their minor differences represent interspecific divergence or intraspecific variation.

Molecular analyses

A total of 50 *Ligidium* sequences were analyzed, including two mitochondrial genes (*COI*, *12S rRNA*) from the nine species identified in the morphological analysis (Suppl. material 1). Phylogenetic analyses based on the concatenated two-gene dataset, using both ML and BI methods, revealed two main clades (Clade A and Clade B) [Fig. 1; maximum bootstrap values (BS) = 100, maximum Bayesian posterior probabilities (PP) = 1]. The main clades corresponded to three species distributed in southeastern China and five species occurring in southwestern China, respectively. Furthermore, the *Ligidium* specimens from Jiangxi and Sichuan – identified as potential new species in the morphological analysis – were strongly supported as distinct lineages with high support values (Fig. 1).

Finally, we treated the two *Ligidium* specimens as valid new species by integrating the morphological and phylogenetic results. The subsequent descriptions and remarks on these new species are provided in the taxonomic section.

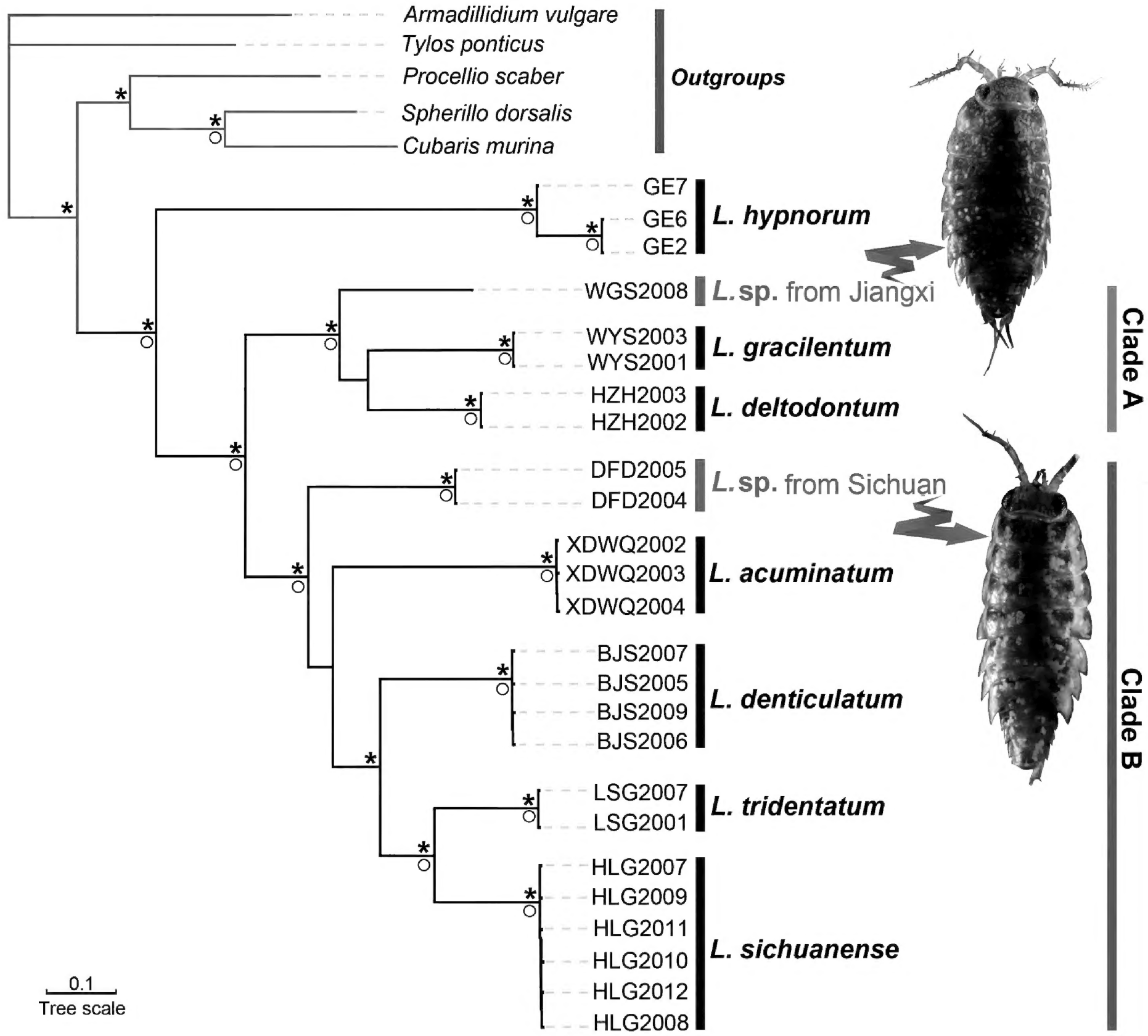

Figure 1. Bayesian consensus tree based on *COI* and *12S rRNA* sequences. Asterisks and circles represent high node support with Bayesian posterior probabilities > 0.95 and maximum bootstrap values > 95. The tree scale represents the number of nucleotide substitutions per site.

Taxonomic account

***Ligidium alpinum* Li & Jiang, sp. nov.**

https://zoobank.org/C9EAA11F-0C44-4BD2-A92D-DDDC1E9ADDFD

Figs 1, 2, 3A

Type material. ***Holotype.*** China • male, Jiangxi Province, Pingxiang City, Wugong Mountain (27°27'N, 114°10'E), alt. 1900 m, 16 September 2012; Weichun Li leg., prep. slide nos. L16002–L16009.

Paratypes. One female, same collection data as holotype, DNA nos. WGS2008.

Diagnosis. Male pleopod 2 endopod has a dagger-shaped distal part and bears four small spines on inner margin.

Description. Maximum length: males 6.0 mm and females 5.5 mm.

Body elliptic, light grey, and bears pale muscle spots on dorsal surface; pereonite 1 without setae on posterior margin (Fig. 1).

Antennula with four aesthetascs at apex of third article (Fig. 2A).

Antenna with flagellum composed of thirteen articles (Fig. 2B).

Mandible with three-toothed incisor in left mandible, lacinia mobilis three-toothed, three penicils between lacinia mobilis and molar process (Fig. 2C); right mandible with three-toothed incisor, lacinia mobilis four-toothed, three penicils between lacinia mobilis and molar process (Fig. 2D).

Maxillule with three stout penicils and single small seta near distal margin of inner lobe; outer lobe with nine apical teeth of various sizes (Fig. 2E).

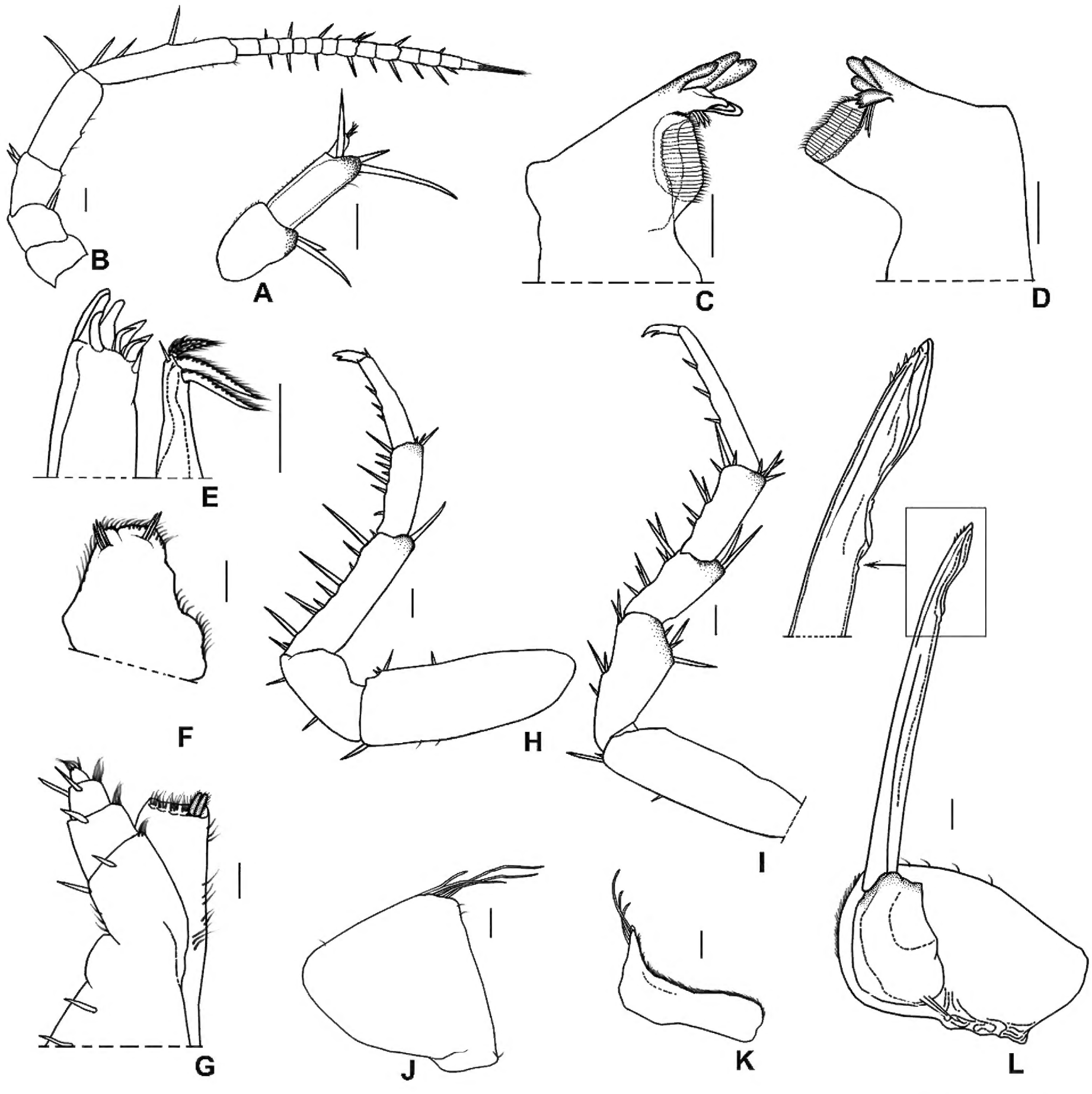

Figure 2. *Ligidium alpinum* sp. nov., holotype. **A.** Antennula; **B.** Antenna; **C.** Left mandible; **D.** Right mandible; **E.** Maxillule; **F.** Maxilla; **G.** Maxilliped; **H.** Pereopod 1; **I.** Pereopod 7; **J.** Pleopod 1 exopod; **K.** Pleopod 1 endopod; **L.** Pleopod 2. Scale bars: 0.1 mm.

Maxilla distally divided into two parts with blunted rounded apices, large lappet with two elongated setose penicils at subapical part, small lappet with three elongated setose penicils near distal margin (Fig. 2F).

Maxilliped endite rectangular, distal margin with two teeth at inner distal angle; palp with seven setae (Fig. 2G).

Pereopod 1 basis with single distal seta on sternal face and four setae on ternal face; ischium with two setae on sternal face and concave on ternal face; merus with twelve setae on sternal face and single seta at distal angle on ternal face; carpus with seven setae on sternal face and three setae at distal angle on ternal face; propodus bears three small setae on sternal face and single small seta at outer distal tip on ternal face (Fig. 2H). Pereopod 7 basis bears three setae on sternal face; ischium narrow basally, broadened towards subtip, then narrowed towards distal tip, bears five setae on sternal face and four setae near tip on ternal face; merus with six setae on sternal face and two setae at distal angle on ternal face; carpus bears seven setae on sternal face and four setae at distal angle on ternal face; propodus bears three small setae on sternal face (Fig. 2I).

Male pleopod 1 exopod with blunted distal apex and bears four long setae; endopod with triangular projection, distal apex with three long setae (Fig. 2J, K). Male pleopod 2 exopod subrectangular; endopod long and thin, distal part dagger-shaped, inner margin with four small spines (Fig. 2L).

Etymology. Latin: *alpinus* = alpine. The new species name refers to its type locality located near the top of Wugong Mountain, the second-highest mountain in east China.

Distribution. This species is only known from Wugong Mountain, Pingxiang City, Jiangxi Province, China.

Figure 3. Natural environment of the collecting locality of *Ligidium* species. **A.** Collecting locality of *L. alpinum* sp. nov.; **B.** Collecting locality of *L. cuspidatum* sp. nov.

Natural history. The habitat in which this species has been collected is near a stream. The vegetation of the collection site is composed of alpine meadows (Fig. 3A).

Remarks. This species is similar to *L. hypnorum*, *L. acuminatum*, and *L. tridentatum* by having a straight distal part of the male pleopod 2 endopod. It can be distinguished by the distal apex of the male pleopod 2 endopod with four small spines on inner margin (Fig. 2L). In *L. hypnorum* and *L. acuminatum*, the male pleopod 2 endopod without spines (Jackson 1923: fig. 4; Wang et al. 2022: fig. 10). In *L. tridentatum*, the inner margin of the male pleopod 2 endopod with three small spines at the subapical apex (Wang et al. 2022: fig. 12). We provided additional molecular evidence to distinguish them. Every species was represented by a well-supported clade (Fig. 1).

Ligidium cuspidatum Li & Jiang, sp. nov.

https://zoobank.org/467DDF7C-4256-48FD-98CB-6BEBA3963DD4

Figs 1, 3B, 4

Type material. ***Holotype.*** China • male, Sichuan Province, Leshan City, Mabian Dafengding National Nature Reserve (28°51'N, 103°31'E), alt. 1100 m, 12 August 2012, Weichun Li and Li Huang leg., prep. slide nos. L15054–L15067.

Paratypes. Two females, same collection data as holotype, DNA nos. DFD2004, DFD2005.

Diagnosis. Male pleopod 2 endopod bears a beak-shaped tooth at approximately distal one-sixth on outer margin and has two small spines near distal apex on inner margin, slender distal part bent outwards and ending with a pointed apex.

Description. Maximum length: males 5.0 mm and females 6.0 mm.

Body elliptic, ochre mixed with dark grey, and bears pale green muscle spots on dorsal surface; pereonite 1 without setae on posterior margin (Fig. 1).

Antennula with one aesthetasc at apex of third article (Fig. 4A).

Antenna with flagellum composed of eleven articles (Fig. 4B).

Mandible with three-toothed incisor in left mandible, lacinia mobilis three-toothed, six penicils between lacinia mobilis and molar process (Fig. 4C); right mandible with three-toothed incisor, lacinia mobilis four-toothed, three penicils between lacinia mobilis and molar process (Fig. 4D).

Maxillule with three stout penicils and one small seta near distal margin of inner lobe; outer lobe with twelve apical teeth of various sizes (Fig. 4E).

Maxilla distally divided into two parts with blunted rounded apices, large lappet with six elongated setose penicils at subapical part, small lappet with four elongated setose penicils near distal margin (Fig. 4F).

Maxilliped endite rectangular, distal margin with two teeth at inner distal angle; palp with six setae (Fig. 4G).

Pereopod 1 basis with two setae on sternal face and single seta at distal angle on ternal face; ischium concave on ternal face; merus with four setae on sternal face and single seta at distal angle on ternal face; carpus with six setae on sternal face and single seta at distal angle on ternal face; propodus bears four small setae on sternal face and single small seta at distal tip on ternal face (Fig. 4H). Pereopod 7 basis bears single distal seta at distal angle on sternal face; ischium narrow and concave basally, broadened towards subtip, then narrowed towards distal tip, bears two setae on sternal face and ternal face, respectively; merus with three long setae on sternal face and two setae at distal angle on ternal face; carpus bears three long setae on sternal face and two setae at distal angle on ternal face; propodus bears three small setae on sternal face (Fig. 4I).

Male pleopod 1 exopod with blunted distal apex, and bears three long setae; endopod with triangular projection, distal apex with three long setae (Fig. 4J, K). Male pleopod 2 exopod subrectangular; endopod long and thin, second segment with outcurve distal part and pointed apex, bears a beak-shaped tooth at approximately distal one-sixth on outer margin, and has two small spines near distal apex on inner margin (Fig. 4L, M).

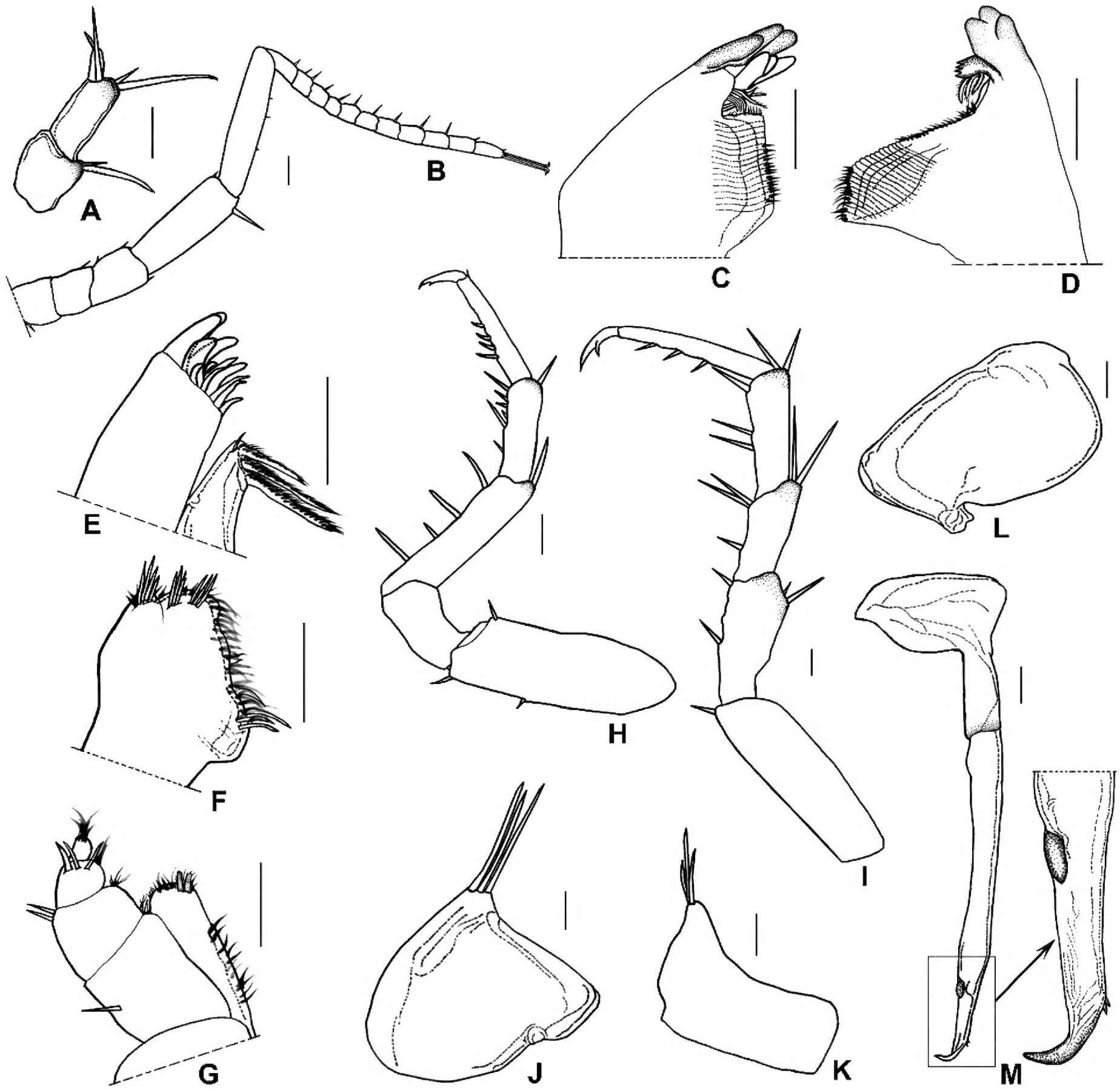

Figure 4. *Ligidium cuspidatum* sp. nov., holotype. **A.** Antennula; **B.** Antenna; **C.** Left mandible; **D.** Right mandible; **E.** Maxillule; **F.** Maxilla; **G.** Maxilliped; **H.** Pereopod 1; **I.** Pereopod 7; **J.** Pleopod 1 exopod; **K.** Pleopod 1 endopod; **L.** Pleopod 2 exopod; **M.** Pleopod 2 endopod. Scale bars: 0.1 mm.

Etymology. Latin: *cuspidatus* = pointed. The new species name refers to the male pleopod 2 endopod with a pointed distal apex.

Distribution. This species is only known from Mabian Dafengding National Nature Reserve, Sichuan Province, China.

Natural history. The habitat in which this species has been collected is under the fallen leaves near a waterfall. The vegetation of the collection site is composed of shrubs and evergreen broadleaf trees (Fig. 3B).

Remarks. This species is similar to *L. denticulatum*, *L. deltodontum*, *L. gracilentum*, and *L. sichuanense* by having a tooth at the distal part of the male pleopod 2 endopod on outer margin. It can be distinguished by the slender and outcurved distal part of the male pleopod 2 endopod with two small spines on the inner margin. In the latter four species, the distal part of the male pleopod 2 endopods without spines on the inner margin (Shen 1949: fig. 26; Li 2017: figs 3, 7; Nunomura 2002: fig. 3). We provided additional molecular evidence to distinguish them. Every species was represented by a well-supported clade (Fig. 1).

Discussion

In the field, *Ligidium* habitats are typically found in wet environments, such as the edges of wetlands (swamps, canals, and streams) or under vegetation near water (Klossa-Kilia et al. 2005; Ferenti and Covaciu-Marcov 2014). The type localities of the new species described

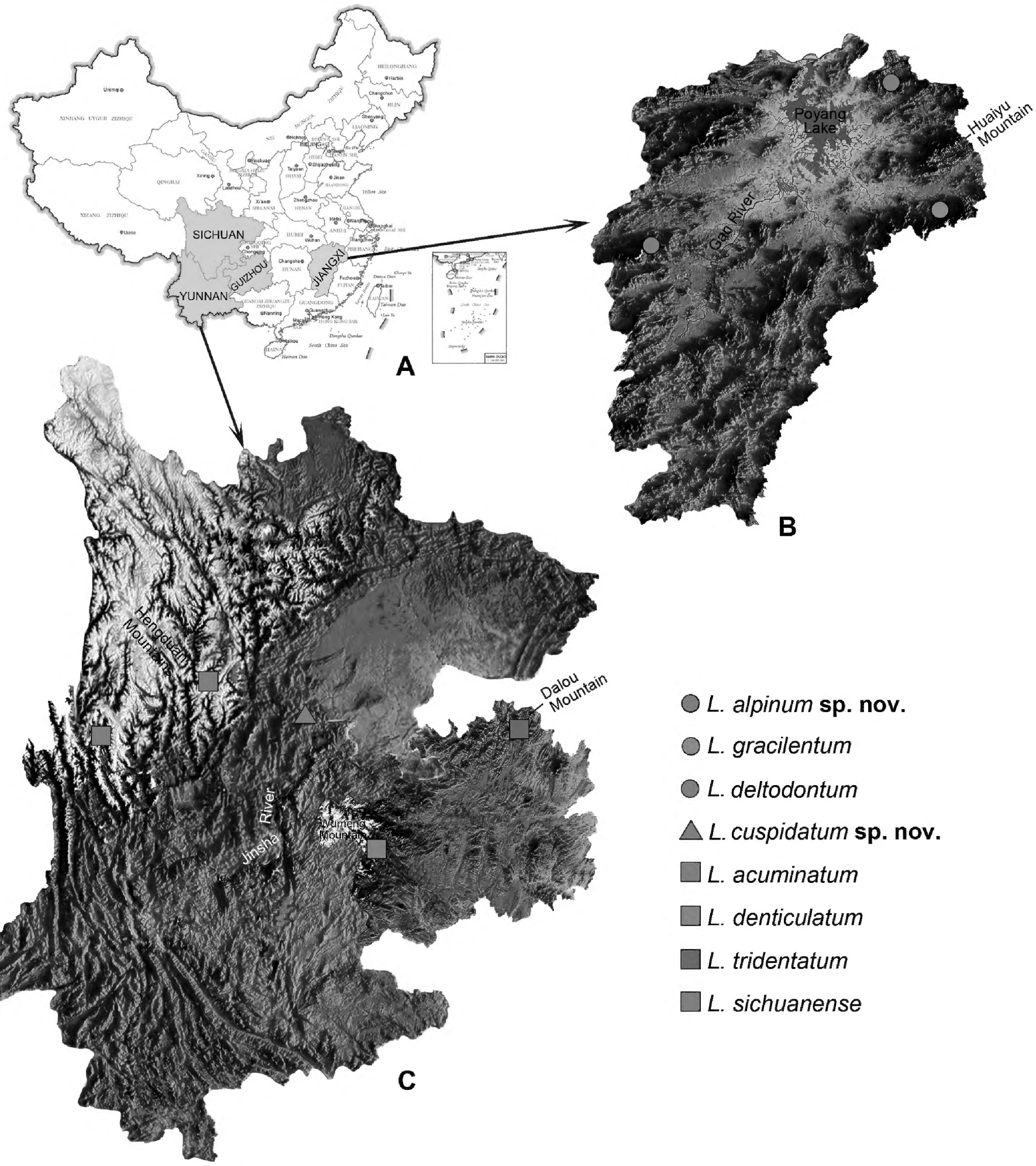

Figure 5. Maps showing the distribution of the studied *Ligidium* species. **A.** China map showing the study regions: Jiangxi Province (shaded green) and three southwestern Chinese provinces (Sichuan, Yunnan, and Guizhou, highlighted in pink); **B.** Topographic map of Jiangxi Province with the distribution of Clade A species; **C.** Topographic map of southwestern China showing distribution patterns of Clade B species.

in this study were also discovered near water sources: specimens of *L. alpinum* sp. nov. were collected beside a mountain stream, and *L. cuspidatum* sp. nov. was found under a waterfall. Previous studies have shown that *Ligidium* species are highly sensitive to environmental humidity, and drought conditions can increase extinction rates within *Ligidium* populations (Klossa-Kilia et al. 2005; Sfenthourakis and Hornung 2018; Harigai et al. 2023). Our field experience confirms that *L. alpinum* sp. nov. is similarly sensitive to habitat changes. We collected *L. alpinum* sp. nov. beside a stream near the summit of Wugong Mountain in 2012. However, the species had disappeared from the collection site when we returned after 2019, as the stream had dried up. Water from the nearby mountaintop streams had been diverted into a cistern to support tourism development, exacerbating drought conditions in the niche of *L. alpinum* sp. nov. and likely leading to its disappearance from the type locality. This highlights the need to balance natural resource utilization with niche preservation. *Ligidium* species, including *L. alpinum* sp. nov., may serve as effective bioindicators of environmental change.

Since Brandt (1833) established the genus *Ligidium*, species identification has primarily relied on external morphology and the structure of appendages. Among these traits, the apical structure of the male pleopod 2 endopod is considered the most reliable diagnostic feature, due to substantial interspecific variation. Other traits, such as the shape of the telson and the arrangement of setae on other appendages, are less effective for diagnosis but can assist in species identification. In recent years, mitochondrial loci have been successfully applied as effective DNA barcodes for delimiting *Ligidium* species (Li 2017; Wang et al. 2022; Recuero and Caterino 2025), providing additional molecular support for species identification. In this study, we revealed two main clades (Clade A and Clade B) and nine species within *Ligidium* based on *COI* and *12S rRNA* data (Fig. 1). The species in Clade A are distributed in southeastern China (Jiangxi Province), while all members of Clade B inhabit southwestern China (Guizhou, Sichuan, and Yunnan Provinces), with each species exhibiting allopatric distributions (Fig. 5). Notably, *L. alpinum* sp. nov. is geographically isolated from *L. deltodontum* and *L. gracilentum* by the Gan River and Poyang Lake, while Huaiyu Mountain separates the latter two species (Fig. 5B). In southwestern China, geographic barriers also occur between species, including the Hengduan Mountains, Jinsha River, Wumeng Mountain, and Daluo Mountain (Fig. 5C). These prominent geographic features have likely played a key role in driving speciation within the genus.

In conclusion, we evaluated the taxonomic status of nine morphologically similar *Ligidium* species by combining morphological examination with molecular phylogenetic analyses based on two mitochondrial genes (*COI*, *12S rRNA*). Our results confirm that the integration of traditional morphological criteria with molecular data is effective for distinguishing closely related woodlice species.

Acknowledgements

We are grateful to Dr. Stefano Taiti (Istituto per lo Studio degli Ecosistemi, Italy), Dr. Noboru Nunomura (Kanazawa University, Japan), Dr. Shigenori Karasawa (Tottori University, Japan), and Dr. Do Heon Kwon (Inje University, Korea) for providing invaluable references and generous assistance. Special thanks are given to Dr. Luiz F. Andrade and two anonymous reviewers for their insightful comments and suggestions on the manuscript. This research was supported by the National Natural Science Foundation of China (Nos. 32460124 and 82474043) and the Key Project at the Central Government Level: Capacity Building for the Sustainable Use of Valuable Chinese Medicine Resources (2060302).

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Supplementary material 1

Supplementary data

Authors: Zili Zong, Jin Wang, Chao Jiang, Weichun Li
Data type: docx
Explanation note: Description of the samples that were used for phylogenetic analysis, including taxon, DNA number, collection localities, DNA Data Bank of Japan (DDBJ)/National Center for Biotechnology Information (NCBI) accession number.

Link: https://doi.org/10.3897/zse.101.148504.suppl1